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DISPROOF OF A CERTAIN TYPE OF THEORIES OF CROSSING OVER BETWEEN CHROMOSOMES¹

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I

Two types of relations have been proposed to account for the facts of "crossing over" between pairs of characters that follow the same pair of chromosomes. One is a varying relation between the substances forming the factors belonging to *diverse pairs* in the same chromosome; the other a varying relation between the *two members of the same pair*, in the two paired chromosomes.

The former type is represented by the "chiasmatype" theory, held by Morgan and his associates, in which the diverse relations are held to be, or depend upon, the actual diverse distances apart of the factors extended along the linear chromosome. When the chromosome breaks, for any cause, it is more likely to separate two factors far apart than two close together; on this depends the varying cross-over ratios.

The second type is that brought to notice recently by Goldschmidt (1917), and commonly called the "variable force" theory. It is conceived that the two members of a given pair, as A and a, in the two paired chromosomes, may be held or drawn to their places by a pair of varying forces, which allow them to exchange places on the average in a certain proportion of cases; while B and b are held by a different pair of forces, which allows these two to interchange in a different proportion of cases; C and c by a still different pair, etc. The result would be diverse

¹ This paper arose and took shape during discussions on theories of crossing over in the Seminary on Genetics at the Johns Hopkins University.

ratios of crossing over when diverse pairs are compared; the cross-over ratio between A-a and B-b would be different from that between A-a and C-c, and so on. It is this theory that I propose to examine. I do not understand that Goldschmidt commits himself to any form of this theory, or to any theory that is exclusively of this type, so that this discussion is not presented as a commentary on his views, but on this type of theory for its own sake. Is it possible to explain the observed ratios of crossing over by any theory of this type?

To grasp the matter clearly, it will help to have an example before us. Let the following twelve groups of letters represent twelve pairs of chromosomes in twelve cells, each chromosome bearing two factors, which we will call A-B and a-b. The upper two letters in each pair show a single chromosome containing the factors A-B, the lower two the mated chromosome containing the factors a-b.

I. AB AB *AB* *AB* AB AB *AB* AB *AB* AB *AB*
 ab ab *ab* *ab* ab ab *ab* ab *ab* ab *ab*

Now suppose that the forces holding A and a to their chromosomes are such that A and a exchange in one fourth of all cases, while B and b exchange in one third of all cases. That is, A and a exchange places in every fourth chromosome pair, B and b exchange places in every third pair. The letters that are thus to exchange with their mates are italicized in the pairs indicated above. The exchanges will evidently give the following result:

II. AB AB Ab aB AB Ab AB aB Ab AB AB ab
 ab ab aB Ab ab aB ab Ab aB ab ab AB
 + + + + +

By a cross-over is meant the fact that two factors of diverse pairs, as A and B, which in the germ cells that formed the parent were following the same chromosome (as in I, above), are found in the germ cells *from* those parents (II, above) to be following diverse chromosomes (as in the third pair of II, above); while conversely the two factors A and b, which were following diverse

chromosomes, are now following the same one. The cross-overs in II, above, are those indicated by the + sign; there are five of these. The ratio of the number of these new combinations (5) to the total number of germ cells (12) is the cross-over ratio; in this case the cross-over ratio is $\frac{5}{12}$, or .417.

Examination of this case will illustrate an important fact. *A cross-over is produced only when one of the two pairs exchanges while the other does not.* In the last pair to the right, in the example given above, the members of both pairs exchange places, but this does not give a cross-over—since A and B are still together, as they were before the double exchange.

Now if the number of exchanges for each pair of cells is different from that in the example given above, the resulting cross-over ratio will be different. By supposing each pair of factors, A-a, B-b, C-c, D-d, etc., to have its own characteristically diverse frequency of interchange of its members, all sorts of cross-over ratios could be obtained, varying from 0 to 1; that is, from no cross-overs to all cross-overs. The question in which we are interested is, could the observed cross-over ratios in such an organism as *Drosophila* be accounted for in this way?

It is to be noted that the problem as we take it up is independent of the nature of the forces that hold A and a (and the other factors) in their places, and that permit them to exchange in a certain proportion of cases. These forces may be utterly heterogeneous in the different cases; they may turn out to be of any kind whatever, so far as this examination goes. We ask merely whether, if the forces, whatever they are, give a constant average proportion of interchanges characteristic for each pair, they can yield the cross-over ratios actually observed.

II

It is evident that on this theory there are two kinds of ratios to be dealt with: the ratio of the number of interchanges of A and a (characteristic for each pair), and the ratio of the number of cross-overs, between two pairs A-a

and B-b; the latter of these ratios depends on the former. We shall call the former the exchange ratio; the latter is commonly known as the cross-over ratio, which we will designate by the letter C.

The exchange ratio signifies the ratio of the number of exchanges between A and a to the total number of germ cells:

$$\text{Exchange Ratio} = \frac{\text{Exchanges}}{\text{Total Number}}$$

The cross-over ratio (C) signifies, of course (following Morgan and the general usage), the ratio of the number of cross-overs to the total number of germ cells or progeny:

$$C = \frac{\text{Cross-overs}}{\text{Total Number}}$$

Goldschmidt (1917, page 90) has given a formula for the cross-over ratio resulting from any two exchange ratios, and has computed the resulting cross-over ratios from certain assumed exchange ratios. We shall give the formula a simpler expression than Goldschmidt has done; one that will enable us to determine its properties and limits of performance.

In cross-over ratios we deal with two pairs of characters, which we may designate A-a and B-b. Let x signify the exchange ratio for one of the pairs; and let y signify the exchange ratio for the other pair. Thus, if A and a interchange in one third of all cases, this pair's exchange ratio x will be one third (or $.33\frac{1}{3}$); while if B and b interchange in two fifths of all cases, its ratio, y , will be two fifths (or $.4$). For convenience we will always choose x and y in such a way that if there is any difference, x will designate the smaller ratio. That is, x will always be equal to or less than y .

Now, suppose that originally the first chromosome of the pairs bears the two factors A and B, the second a and b (as in I, above). After crossing over in the proportion

x , we shall have, in these first chromosomes of the pair, A and a in the following proportions:

$$\begin{array}{c} xa \\ (1-x)A \end{array}$$

Similarly, in this same chromosome we shall find B and b distributed in the following proportions:

$$\begin{array}{c} yb \\ (1-y)B \end{array}$$

(Thus, if A and a interchange in two fifths of all cases, then after interchange we shall, in the first chromosome, find a in two fifths of the cases, A in three fifths; and similarly for B .)

What will then be the proportions of the various combinations of the two pairs of factors? It will evidently be

$$\begin{array}{l} xa + (1-x)A, \text{ multiplied by} \\ \frac{yb + (1-y)B}{= xyab + x(1-y)aB + y(1-x)Ab} \\ + (1-x)(1-y)AB \end{array}$$

The cross-overs are aB and Ab , the proportion of which is evidently:

$$x(1-y) + y(1-x) = x + y - 2xy$$

The same result will be reached if we consider the second chromosome of each pair (that which originally contained a and b); so that the same proportion holds for both together. This, therefore, gives us our formula for the cross-over ratio in terms of the exchange ratios of the two pairs. It is essentially the same formula employed by Goldschmidt (1917), giving the same results, but written in more perspicuous form.

Let us therefore recapitulate in algebraic form the essential points.

Let

x = exchange ratio of one pair,

y = exchange ratio of other pair

(so selected that $x \equiv y$).

Then for the cross-over ratio (C) of the two pairs, the formula is

$$C = x + y - 2y.$$

An example or two will make the use of this formula clear. Suppose that the exchange ratio of pair A-a is $\frac{3}{7}$; of B-b it is $\frac{2}{5}$. Then

$$x = \frac{2}{5}; \quad y = \frac{3}{7}$$

$$C = \frac{2}{5} + \frac{3}{7} - 2(\frac{2}{5} \cdot \frac{3}{7}) = \frac{17}{35} = .486$$

Again, let

$$x = .31, \quad y = .34$$

$$C = .31 + .34 - 2(.31 \times .34) = .439$$

(It is customary to express the results as percentages; thus the last example would give a cross-over ratio of 43.9 per cent. For our purposes it is more convenient to leave them as decimals.)

Now this formula has certain characteristics and limitations that allow us to bring the theory on which it is based to a test. The theory is that each pair has its characteristic exchange ratio; if that be the case, this formula holds.

We shall set forth certain of the important relations between cross-over ratio and exchange ratios, revealed by this formula; then show how these provide a test for the theory which the formula expresses. To aid in the comprehension of these relations, we give a table showing all cross-over ratios for two pairs of characters, resulting from the combinations of exchange ratios varying by tenths from 0 (no exchange) to 1 (all exchange). The table illustrates all the relations to be deduced from the formula.

		Exchange Ratio for One Pair (A-a).										
		0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
Exchange Ratio for the Other Pair (B-b).	.0	0	.10	.20	.30	.40	.50	.60	.70	.80	.90	1.00
	.1	.10	.18	.26	.34	.42	.50	.58	.66	.74	.82	.90
	.2	.20	.26	.32	.38	.44	.50	.56	.62	.68	.74	.80
	.3	.30	.34	.38	.42	.46	.50	.54	.58	.62	.66	.70
	.4	.40	.42	.44	.46	.48	.50	.52	.54	.56	.58	.60
	.5	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50
	.6	.60	.58	.56	.54	.52	.50	.48	.46	.44	.42	.40
	.7	.70	.66	.62	.58	.54	.50	.46	.42	.38	.34	.30
	.8	.80	.74	.68	.62	.56	.50	.44	.38	.32	.26	.20
	.9	.90	.82	.74	.66	.58	.50	.42	.34	.26	.18	.10
	1.0	1.00	.90	.80	.70	.60	.50	.40	.30	.20	.10	0

EXPLANATION OF THE TABLE

Table of the values of the cross-over ratios resulting from combinations of different exchange ratios, from 0 to 1, of two pairs of factors. Based on the formula:

$$C = x + y - 2xy$$

Where x = the exchange ratio of one pair,

y = the exchange ratio of the other,

and $x \leq y$.

Outside the square (above and to the left) are the exchange ratios, by tenths, from 0 to 1; within are the cross-over ratios. To find the cross-over ratio resulting from any two exchange ratios, trace the rows and columns of figures from the two exchange ratios till they intersect; thus the cross-over ratio resulting from an exchange ratio in one pair of .6, in the other of .3, is .54.

The table shows directly the limiting values for the cross-over ratios from any two exchange ratios that are not exactly the same as those of the table. Thus:

If the upper left quadrant:

If x or y or both are below the values given in the table, the cross-over ratio is below the value given in the table. Thus if x is below .2 and y is below .3, the cross-over ratio is below .38. If both are below .10, the cross-over ratio is below .18.

If x or y or both are above the values given in the table, the cross-over value is above that given in the table.

In the lower right-hand quadrant:

If x or y or both are above the values in the table, the cross-over value is *below* that given in the table.

If x or y or both are below those in the table, the cross-over value is above that of the table.

In the other two quadrants (upper right and lower left):

If x is smaller and y larger than in the table, the cross-over ratio is above that of the table.

If x is larger and y smaller than in the table, the cross-over value is below that of the table.

Example: x and y given; limits of C required:

$$x = .16, \quad y = .29; \quad C < .38 \text{ and } > .26$$

$$x = .09, \quad y = .08; \quad C < .18 \text{ and } > .0$$

$$x = .13, \quad y = .73; \quad C < .74 \text{ and } > .62$$

$$x = .54, \quad y = .63; \quad C < .50 \text{ and } > .48$$

C given; limits of x and y required:

$$C = .434, \quad x \text{ and } y \text{ both } \geq .434, \text{ or both } \leq .566$$

$$C = .021, \quad x \text{ and } y \text{ both } \geq .021, \text{ or both } \leq .979$$

$$C = .63; \quad x \leq .37 : y \leq .63$$

$$C = .96; \quad x \leq .04 : y \leq .96$$

$$C = .50; \quad x = .50 : y = \text{any value from } 0 \text{ to } 1.$$

The formula for examination is:

$$C = x + y - 2xy$$

(in which x and y are proper fractions).

1. Two exchange ratios, x and y , give the same cross-over ratio (C) as do their complements, $1 - x$ and $1 - y$. For

$$x + y - 2xy = (1 - x) + (1 - y) - 2(1 - x)(1 - y),$$

as will be seen by performing the operations indicated in the second member of the equation. But this second member is the value of C for exchange ratios $1 - x$ and $1 - y$.

For example, the two exchange ratios .2 and .3 give the same cross-over ratio as do the two exchange ratios .8 and .7; for both cases $C = .38$. This relation is seen in the symmetrical constitution of the table; the cross-over ratio resulting from .1 and .2 is the same as that from .9 and .8; the cross-over ratio resulting from exchange ratios .4 and .7 is the same as that resulting from .6 and .3, etc. The rule holds equally for values not found in the table; thus the cross-over ratio resulting from .011

and .031 is the same as that resulting from .989 and .969.

2. If one of the two exchange ratios is changed to its complement, the cross-over ratio is changed to its complement.

That is, if the cross-over ratio resulting from x and y is C , the cross-over ratio resulting from x and $1 - y$, or y and $1 - x$ is $1 - C$.

For:

$$x + (1 - y) - 2x(1 - y) \equiv 1 - (x + y - 2xy)$$

But the first member of this equation is the cross-over ratio from x and $1 - y$, while the second member is 1 minus the cross-over ratio from x and y . The same result is reached if we take y and $1 - x$.

Thus, as the table shows, the cross-over ratio resulting from .2 and .3 is .38, so that the cross-over ratio from .2 and .7 is .62, as is likewise the cross-over ratio from .8 and .3 (.38 + .62 = 1). Similarly, the cross-over ratio of .011 and .031 is .0413; hence the cross-over ratio from .011 and .969 is .9587.

3. When the cross-over ratio is less than $\frac{1}{2}$, the exchange ratios x and y are either both greater than $\frac{1}{2}$ or both less than $\frac{1}{2}$; one can not be less than $\frac{1}{2}$, the other greater. That is:

If $C < \frac{1}{2}$ then either $x < \frac{1}{2}$ and $y < \frac{1}{2}$ or $x > \frac{1}{2}$ and $y > \frac{1}{2}$. For let us suppose that $x = \frac{1}{2} - a$ and $y = \frac{1}{2} + b$, in which a and b are any positive quantities. Then $C = x + y - 2xy = \frac{1}{2} + 2ab$. Therefore x can not be less than $\frac{1}{2}$ and y more than $\frac{1}{2}$.

On the other hand, if $x = \frac{1}{2} - a$ and $y = \frac{1}{2} - b$, or if $x = \frac{1}{2} + a$, $y = \frac{1}{2} + b$; in either case $C \equiv x + y - 2xy = \frac{1}{2} - 2ab$. So that in these cases the cross over-ratio C is less than $\frac{1}{2}$.

4. Conversely to 3, when the exchange ratios x and y are both less than $\frac{1}{2}$, or when they are both more than $\frac{1}{2}$, the cross-over ratio is less than $\frac{1}{2}$.

That is, when $x < \frac{1}{2}$ and $y < \frac{1}{2}$, or when $x > \frac{1}{2}$ and $y > \frac{1}{2}$; in either case $C < \frac{1}{2}$. This was proved under 3.

5. When the cross-over ratio is greater than $\frac{1}{2}$, one ex-

change ratio is less than $\frac{1}{2}$, the other greater than $\frac{1}{2}$. That is: If $C > \frac{1}{2}$, then $x < \frac{1}{2}$, $y > \frac{1}{2}$. This also was proved under 3.

6. Conversely to 5, when one exchange ratio is less than $\frac{1}{2}$, the other greater than $\frac{1}{2}$, the cross-over ratio is greater than $\frac{1}{2}$. That is: If $x < \frac{1}{2}$, $y > \frac{1}{2}$, then $C > \frac{1}{2}$. This also was proved under 3.

All these relations are evident in the table.

7. When the cross-over ratio is less than $\frac{1}{2}$, the two exchange ratios are either both equal to or less than the cross-over ratio; or both equal to or more than the complement of the cross-over ratio. They can not have any value lying between the cross-over ratio and its complement. That is: When $C < \frac{1}{2}$, either x and y each $\equiv C$ or x and y each $\equiv 1 - C$.

This is an extremely important principle, on which the final test of the theory depends. It is proved as follows:

In 3 we saw that if the cross-over ratio is less than $\frac{1}{2}$, either x and y are both less than $\frac{1}{2}$; or both of them are greater than $\frac{1}{2}$.

(a) Let us take first the case where x and y are each less than $\frac{1}{2}$. In this case, in the formula $C = x + y - 2xy$, the quantity $2xy$ is smaller than x , and smaller than y . For since x is less than $\frac{1}{2}$, $2x$ is less than 1, whence it follows that $2xy$ is less than y ; and the same reasoning shows that $2xy$ is likewise smaller than x . Hence the formula for C subtracts from the sum of x and y a quantity smaller than y ; it therefore leaves a quantity larger than x ; and the same reasoning shows that it leaves a quantity larger than y . Only in the limiting case that $x = 0$ does $y = C$.

(b) Take next the other possible case, in which x and y are both greater than $\frac{1}{2}$. In this case $1 - x$ and $1 - y$ are both less than $\frac{1}{2}$. Thence it follows (by the reasoning just employed) that

$$(1 - x) + (1 - y) - 2(1 - x)(1 - y)$$

is greater than $1 - x$ and greater than $1 - y$. But, as was seen in (1),

$$(1-x) + (1-y) - 2(1-x)(1-y) = x + y - 2xy \equiv C$$

So that in this case $C > 1-x$ and $C > 1-y$.

Thus the fraction C is nearer to 1 than the fraction $1-x$. If therefore we subtract the fraction C from 1, it will leave a smaller number than if we subtract the smaller fraction $1-x$ from 1. That is: $1-C < x$.

And in the same way it can be shown that $1-C < y$. Only in the limiting case that $y=1$ does $x=1-C$.

The general principle in this section can be expressed as follows:

When the cross-over ratio is less than $\frac{1}{2}$, the two exchange ratios, x and y , either both differ from 0 by less than the cross-over ratio, or both differ from 1 by less than the cross-over ratio.

This relation is well seen in the table. For example, for the cross-over ratio .38 the two exchange ratios are either .3 and .2 (both less than .38), or they are .8 and .7 (both greater than .62, the complement of .38).

8. Conversely to 7:

If both exchange ratios, x and y , are less than $\frac{1}{2}$, both are equal to or less than the cross-over ratio.

If both exchange ratios, x and y , are greater than $\frac{1}{2}$, both are equal to or greater than the complement ($1-C$) of the cross-over ratio.

9. When the cross-over ratio C is above $\frac{1}{2}$, one of the exchange ratios (x) is equal to or less than the complement of the cross-over ratio ($1-C$), while the other (y) is equal to or more than the cross-over ratio (C).

Or otherwise expressed:

When the cross-over ratio is above $\frac{1}{2}$, one of the exchange ratios (x) differs from 1 by an amount equal to or more than the cross-over ratio, while the other (y) differs from 0 by an amount equal to or more than the cross-over ratio. That is, when $C > \frac{1}{2}$, $1-x \equiv C$, $y \equiv C$, or $x \equiv 1-C$, $y \equiv C$.

This can be proved by methods similar to those employed in 7.

10. Conversely to 9:

When one exchange ratio (x) is less than $\frac{1}{2}$, the other (y) greater than $\frac{1}{2}$, the cross-over ratio can not be greater than y nor than $1 - x$:

If $x < \frac{1}{2}$ and $y > \frac{1}{2}$, $C \equiv y$, $C \equiv 1 - x$.

All these relations 1 to 10 are clearly illustrated in the table.

III

These relations being established, we may turn to a test of the theory by the facts. Do the cross-over ratios experimentally established in such an organism as *Drosophila* show the relations which this theory requires?

Some of the cross-over ratios determined by Morgan and his associates for various pairs of factors in the sex chromosome of *Drosophila* are the following (taken from the list given by Morgan and Bridges, 1916, page 84).

No. of cases examined	Factors	Cross-over Ratio
81,299.....	Yellow-White011
6,461.....	White-Rudimentary424
1,456.....	Rudimentary-Forked014
2,563.....	Yellow-Rudimentary429
13,271.....	Yellow-Vermilion345
10,155.....	Vermilion-Miniature031
12,786.....	Miniature-Rudimentary179
626.....	Yellow-Bar479
8,768.....	Bar-Fused025
5,955.....	White-Bar436

The cross-over ratio for yellow-white, as shown above, is .011. Therefore, on the theory with which we are dealing, according to principle 7, given above, the exchange ratio for yellow is either equal to or less than .011; or else it is equal to or greater than .989. It can not lie between these numbers. (The same is of course true for the factor white.)

Further, the cross-over value for vermilion-miniature is .031, whence it follows from 7 that the exchange ratio for vermilion is equal to or less than .031, or it is equal to or greater than .969. It can not lie between these values.

What then are the possible cross-over values for yellow-vermilion?

If we give both these factors their maximum exchange ratios lying below $\frac{1}{2}$ (that is .011 and .031), or their minimum exchange ratios lying above $\frac{1}{2}$ (that is, .989 and .969), then work out the cross-over ratio by the formula: $C = x + y - 2xy$, we obtain the same result; the cross-over ratio yielded is .041. But as our list shows, this is less than $\frac{1}{8}$ the actual value, which is .345. If we decrease the two low ratios, or increase the two high ones (which are the only changes the theory allows), the cross-over ratio becomes still less and still farther from the reality.

Suppose then we try giving one factor its possible exchange ratio above $\frac{1}{2}$, the other its possible exchange ratio below $\frac{1}{2}$. But we know already, by 6, that this will give us a cross-over ratio above .50, whereas the actual ratio is but .345. If we actually work out the ratios, we find that the minimum cross-over ratio that we can obtain in this way is .959, in place of the actual .345.

Thus on this theory the only cross-over ratios that the pair yellow-vermilion can have, consistently with the values of the cross-over ratios yellow-white and vermilion-miniature, either lie below .041 or above .959; yellow-vermilion can not have a cross-over ratio lying between these values. Yet the actual value (from the study of 13,271 cases) is .345.

This example is typical. We shall come to the same kind of a result if we examine many other cross-over ratios in *Drosophila*. For example, we find that yellow-white yield the ratio .011; rudimentary-forked the ratio .014. It follows from this that the cross-over ratio for white-rudimentary either lies below .025 or above .975; on this theory it can not lie between these values. Yet its actual value is .424—very near the middle of the region of values which the theory does not permit it to hold. And similarly for other pairs. It is a necessary consequence of this theory that if two factors each give with any other factors extreme cross-over ratios (very

high or very low), they can not together give cross-over ratios of the more intermediate values. For example (as our table shows), if two factor pairs each give, with any other, cross-over ratios below .10, they can not give together a cross-over ratio lying anywhere between .18 and .84. If the two pairs each yield any cross-over ratios lying below .20, they can not give together a cross-over ratio lying between .32 and .68. These and many similar relations, illustrated in the table, are inherent in the theory we are considering, but are completely opposed to what is found in nature.

IV

These facts completely refute any theory which holds that the observed constant cross-over ratios between pairs of factors are the result of constant exchange ratios between the two members of a given pair—exchange ratios that are characteristically diverse for the different pairs (such theories as that outlined by Goldschmidt, 1917). The refutation is independent of the question of the nature of the forces involved; whatever the forces, if they give constant average exchange ratios for each pair, the results are bound to be inconsistent with the observed cross-over ratios. No theory will hold that does not provide for diverse relations between the different factors in the same chromosome, such that some tend to cling together more frequently than others.

Possibly some elements of the theory that diverse exchange ratios are characteristic for different pairs might be retained, if there be added provision for modification of the exchange ratio in a given pair, depending on whether or not exchange occurs in some other pair. It might be held, for example, that *A* and *a* are more likely to exchange if in the same cell *B* and *b* have exchanged; or the reverse. This would give a theory of mixed type, which added to the forces regulating the exchange between two members of a pair, other forces causing two given pairs to tend to do the same thing, or the opposite

thing. The "variable force" theory would therein approach the chiasmotype theory, in which the diverse relations between the factors belonging to different pairs are the primary, if not the exclusive, elements considered.

As theories of other type become successively modified so as to take into account the known facts: the fact that the chromosome actually is a linear aggregate; the fact that the two chromosomes while in this linear condition pair and intertwine; the fact that cross-overs occur only at the period when this occurs; the fact that two recessive allelomorphs when mated do not produce normals, while two recessives not allelomorphs do; the fact that after two factors, A and B, are found to hold together in one generation, if we mate their cross-overs $A-b$ and $a-B$, we now find that it is A and b , not A and B that tend to hold together (Bridges, 1917); the fact that when a given factor is lost from a chromosome, others that have low cross-over ratios with that factor are also lost (Bridges, 1917a);—when the modifications required for bringing these facts into relation with each other and with others are introduced, it appears that the resulting theory will come more and more to resemble the chiasmotype theory. No theory is adequate that does not include and bring into relation the facts just mentioned, for a correct theory is nothing but a presentation of the facts in their correct (verifiable) relations.

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